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► To cite this version:

Pieter de Frenne, Florian Zellweger, Francisco Rodríguez-Sánchez, Brett Scheffers, Kristoffer Hylander, et al.. Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 2019, 3 (5), pp.744-749. 10.1038/s41559-019-0842-1 . hal-02352625

HAL Id: hal-02352625

<https://hal.science/hal-02352625>

Submitted on 13 Nov 2019

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Global buffering of temperatures under forest canopies

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24 **Abstract**

25 Macroclimate warming is often assumed to occur within forests despite the potential for tree cover
26 to modify microclimates. Using paired measurements (under the canopy vs. in the open) at 98 sites
27 across five continents, we show that forests function as a thermal insulator, cooling the understory
28 when ambient temperatures are hot and warming when ambient temperatures are cold. The
29 understory vs. open temperature offset is magnified as temperatures become more extreme and is of
30 greater magnitude than the warming of land temperatures over the past century. Tree canopies may
31 thus reduce the severity of warming impacts on forest biodiversity and functioning.

32 **Main text**

33 Biological impacts of macroclimate warming are increasingly evident across a wide array of
34 ecosystems¹⁻⁵. Many responses of biological communities and ecosystem processes, however, are
35 lagging behind warming of the macroclimate⁶⁻¹¹. Such time lags may be the inevitable consequence
36 of slow dispersal and demography^{3, 7, 8}, but may also be due to the buffering of localized
37 microclimates by vegetation and topography, such that organisms do not necessarily experience the
38 same degree of warming as measured at weather stations¹²⁻¹⁸. Biotic and abiotic features near the
39 ground create heterogeneous microclimates, mostly via effects on radiation, air mixing,
40 evapotranspiration and soil properties, all of which can influence biodiversity and ecosystem
41 functioning^{17, 18}.

42 To better predict the biotic consequences of climate change, we need to further our
43 understanding of how the local temperature experienced by living organisms (referred to as the
44 ‘microclimate’) changes in space and time. Macroclimates outside forests (sometimes referred to as
45 ‘free-air temperatures’ in the literature) are characterized by an extensive global network of weather
46 stations established in the well-mixed air of open areas (e.g. short grasslands) *c.* 2 m above the soil
47 surface^{19, 20} — habitat conditions that are not representative of the conditions experienced by the
48 majority of terrestrial species on Earth^{21, 22}. The study of microclimates is not new, since
49 microclimatological measurements began more than a century ago, but most climate-change studies
50 rely on weather station data that are specifically designed to correct for these microclimatic effects¹⁵⁻
51 ²⁰. Hence, future projections of climate change relying solely on macroclimate ignore the potential
52 impact of microclimates on biodiversity and ecosystem functioning^{1, 2, 5}.

53 Microclimates are particularly evident in forests, where the large majority of species live
54 underneath the canopy of trees that strongly influences local thermal conditions¹⁰⁻¹³. This is of major

55 concern for global-change science because forests cover one-quarter of the Earth's land surface and
56 harbor two-thirds of all terrestrial biodiversity²⁰⁻²³, and some studies have already shown that
57 microclimatic buffering can mediate the response of forest communities to climate change⁸⁻¹¹.

58 Here we report a systematic, global meta-analysis quantifying the thermal buffering capacity of
59 the Earth's dominant forested ecosystems (tropical to boreal forests) across five continents (Fig. 1).
60 Drawing on empirical studies with a strictly paired design (i.e. comparing microclimate with
61 macroclimate), we quantify the average temperature offset of forests and also how the magnitude of
62 such offsets depends on the macroclimatic context (i.e. outside forests). From a total of 98 sites and
63 74 studies, we retrieved paired temperature time series and/or summary statistics (i.e. minimum,
64 mean, or maximum temperatures) for exactly the same time period in (i) understory conditions in
65 forests (i.e. microclimate) and (ii) an adjacent open habitat without shade (i.e. macroclimate). Offset
66 values were always calculated as temperatures inside minus macroclimate temperatures outside
67 forests such that negative values reflect cooler forest temperatures.

68 In our global analysis of 714 paired temperature data, we found that tree canopies buffer
69 forest floors against both high and low macroclimatic temperatures. Mean and maximum understory
70 temperatures were, on average, cooler by 1.7 ± 0.3 and 4.1 ± 0.5 °C (mean \pm S.E., mixed-effects
71 models: both $P < 0.001$) than macroclimate temperatures, respectively. Conversely, minimum
72 temperatures of the forest understory were 1.1 ± 0.2 °C warmer than the macroclimate outside the
73 forest (mixed-effects model: $P < 0.001$; Fig. 1, Supplementary Figs. 1-2). Thus, forest understories
74 are not only cooler on average than nearby open habitats, but negative maximum temperature
75 offsets (cooler in forests) and positive minimum temperature offsets (warmer in forests) also
76 indicate lower temperature variation below the forest canopy.

77 Across the globe, the thermal offset of forests was negatively correlated with the macroclimate
78 temperature outside forests. Thermal offsets became more negative (i.e. lower temperatures in
79 forests) as macroclimate temperature increased, and more positive (i.e. higher temperatures in
80 forests) as macroclimate temperature decreased (Fig. 2a, Supplementary Figs. 3-4). The cooling of
81 mean and maximum temperatures was highest in tropical forests (probably partly as a result of the
82 latitudinal gradient in macroclimate temperatures; Fig. 2a) while minimum temperatures were highest
83 in boreal forests, relative to the macroclimate temperature (Fig. 2b). This means that the latitudinal
84 gradient of forest-floor temperatures is less steep than the latitudinal gradient in macroclimate
85 temperature and that the amplitude of change within a given microhabitat does not always equate to
86 the amplitude of macroclimate change¹¹.

87 To control for the effects of spatiotemporal changes in macroclimate temperatures (e.g.
88 sampling of tropical *vs.* boreal forests, low *vs.* high elevations or warm *vs.* cold years) on the
89 magnitude of the offset, we computed macroclimate temperature anomalies relative to the average
90 conditions over the period 1970-2000 for each of the 98 study sites, and subsequently used it as a
91 predictor variable instead of actual temperatures outside the forest reported in the original studies.
92 The results are in line with those using raw temperature values rather than anomalies: the cooling
93 effect on maximum and mean temperatures, as well as the warming effect on minimum
94 temperatures, are consistent along the gradient of temperature anomalies, with very similar slope
95 estimates compared to the models with actual macroclimate temperatures (Supplementary Fig. 5).

96 Together, these results suggest that the thermal offsetting capacity of forests across the globe
97 may translate into lower warming in the forest understory compared to warming trends using
98 weather-station data from non-forested areas. Forests across the globe are thus effectively serving as
99 a thermal insulator compared with open areas, with such a buffering effect potentially reducing the

100 severity of climate change impacts on forest ecosystems. The offset values we report here now have
101 to be compared to the thermal sensitivities of species and ecosystem processes to better predict
102 ecological responses to increasing temperatures.

103 In addition to spatiotemporal variability, we also tested for additional factors that might
104 explain some of the variation among studies in the magnitude of temperature offsets, such as forest
105 composition (evergreen, mixed or deciduous), tree height, topography, distance to the coast, or the
106 height of the temperature sensors (e.g. aboveground or belowground) (Supplementary Figs. 6-7;
107 Supplementary Table 5). Sensor height indeed impacted the magnitude of the offset: the buffering in
108 forests was strongest close to the ground while the difference in temperatures between forests and
109 open habitats disappeared higher up above-ground, both for minimum and maximum temperatures
110 (Supplementary Fig. 7). Contrary to what we expected based on the scientific literature²⁴, we did not
111 detect an effect of the type of dominant tree species (evergreen, deciduous or mixed), topography,
112 distance to the coast or forest height on the offset; more targeted studies will be needed to provide
113 stronger tests of such factors.

114 Paleoecological records show that temperature changes of greater magnitude and rate have
115 stronger biological consequences^{5, 25}. Here we have shown that microclimate buffering in forests has
116 the potential to partly offset the warming experienced in the forest understory due to anthropogenic
117 climate change, effectively reducing the severity of impacts from heating of the atmosphere. As
118 such, closed forest canopies might provide a line of defense against the impacts of current and
119 future warming on the ecological processes that influence forest ecosystems (e.g. tree regeneration,
120 demography and community reshuffling, litter decomposition, and soil water and nutrient cycling).
121 In addition, because offsetting was strongest for maximum temperatures, we might expect extreme
122 events such as heat waves to be more strongly attenuated than gradual temperature changes.

123 Our results underpin a neglected function of forests: an offset of within-forest temperatures
124 that is of greater magnitude than the global warming of land and ocean temperatures over the past
125 century (~0.85 °C, ref. 4) and also the warming of regional surface temperatures following
126 deforestation (usually < 1 °C, ref. 26). Forest canopies serve as thermal insulating layers, likely
127 offsetting the impacts of anthropogenic climate change in the understory, where a large share of
128 forest biodiversity resides and key ecosystem processes take place^{21,22}. It is thus essential to
129 incorporate microclimates into biodiversity and climate science as well as into forest management
130 and policy. As forest loss, degradation, and conversion to monoculture crops continues^{27,28}, human
131 land use might undermine ecosystems' natural ability to mediate climate warming (a positive
132 feedback). Such feedbacks to climate systems may be further exacerbated via effects of
133 microclimates on soil CO₂ and CH₄ fluxes and sub-canopy evapotranspiration rates²⁹.

134 Advances in studies of micro- vs. macroclimate change have thus far been limited by the
135 availability of suitable spatial data to model and map small-scale heterogeneity of microclimate
136 conditions^{10-17,24}. Our global analysis shows the importance of forests in moderating climate
137 warming, and the next step will be to incorporate fine-grained thermal variability into bioclimatic
138 modelling of future species demography and distributions¹⁴⁻¹⁷. Our findings indicate that well-
139 quantified microclimates are key to improving predictions of climate-change impacts and assisting
140 management decisions. Forest managers and policy makers alike can potentially exploit microclimate
141 buffering as a regulating service when developing mitigation and adaptation plans to safeguard forest
142 biodiversity and functioning as well as human well-being in a future, warmer world.

143 **Methods**

144 Literature search and data extraction

145 We performed a literature search on ISI Web of Science to compile suitable published studies
146 assessing the thermal offsetting capacity of forest ecosystems. This search was updated until 15 June
147 2017 and performed by each of three authors (PDF, FZ, JL) independently, using keywords such as
148 microclimat*, microrefug*, microhabitat*, forest*, temperature* and buffer*. The combined number
149 of potentially suitable papers found by these three independent searches was 706. We then screened
150 the titles and abstracts to find studies that potentially met our requirements for data extraction (see
151 the next paragraph). We considered forest microclimates to represent the suite of climatic conditions
152 measured in localized areas near the ground and within the forest understory (below tree canopies).
153 Microclimatic conditions include temperature, precipitation, wind and humidity, but the focus here
154 was on the temperature of the air layer below tree canopies and the temperature of the topsoil due
155 to their importance for the responses of forest organisms and ecosystem functioning to
156 macroclimate warming. The macroclimate was considered as the climate in free-air conditions,
157 representative of a large geographic region without direct canopy effects. This definition follows the
158 definition used by meteorologists who record synoptic or macroclimate conditions from
159 standardized weather stations¹⁹⁻²⁰.

160 Our criteria for study inclusion were the following: studies had to report temperature values
161 (time series or summary statistics such as minimum, mean or maximum values) according to a
162 strictly paired design comparing microclimate below trees (inside forests) with temperatures
163 recorded from a reference neighbouring site outside the forest without any influence of trees (i.e.
164 macroclimate conditions). Reference sites were either a nearby open site equipped with the same
165 type of (shielded) temperature loggers, a nearby weather station (as long as the distance did not
166 confound with the temperature offset of the canopy, e.g. due to significant topographic differences),

167 or a logger placed above the upper canopy surface. Constancy of the location of temperature sensors
168 within a pair of observations (e.g. forest soil temperatures were only compared with control soil
169 temperatures) was a requirement. Temperature data presented in tables or text were entered directly
170 into our database. Temperature data not available directly in the text, raw data or as tables but
171 presented in figures in the original papers (42.3 % of the total number of offset values) were
172 extracted using the digitalization software *WebPlotDigitizer*
173 (<https://automeris.io/WebPlotDigitizer/>). We did not set any limit on the study duration, i.e. we
174 extracted data from studies that quantified paired temperature time series during single days up to
175 several years. If studies were performed along an edge-to-core transect, we only considered the
176 measurements outside the forest farthest away from the edge versus the measurement closest to the
177 core of the forest (as far away from the edge as possible). We screened the titles and abstracts of all
178 above-mentioned 706 publications. In addition, we included a formal process of scanning references
179 lists of relevant papers and further added potentially relevant papers extracted from these reference
180 lists. In total, we identified 74 studies published between 1939 and 2017 that met our above-
181 mentioned requirements for data extraction. The majority of the studies were reported in peer
182 reviewed journal articles, but also 2 PhD theses, 1 book and 2 institutional reports were included.

183 When raw temperature data were available, we computed three summary statistics: maximum,
184 mean and minimum temperatures across time. If available, we extracted temperatures outside and
185 inside the forest and then calculated the magnitude of the offset as understory temperature minus
186 temperature outside the forest; negative values thus reflect cooler temperatures below tree canopies
187 while positive values reflect warmer understory temperatures. A third of the studies (34 % of offset
188 values) only reported the macroclimate vs. understory temperature difference (and not the forest and
189 macroclimate temperatures separately). In these instances, only the offset value itself was directly
190 entered in our database. Replicate forest sites (at least several kilometers apart), seasons

191 (meteorological seasons, later aggregated to growing vs. non-growing season) and temperature
192 metrics (maximum, mean, minimum, air or soil temperatures) within the same study were entered on
193 different rows into the database. Temperature values of longer time series were always aggregated
194 per season and/or year.

195 All authors contributed to the data extraction from the original papers. After the first data
196 extraction, however, all entries into the database were thoroughly double-checked by four authors
197 (PDF, FZ, FRS, JL), working together closely to resolve any discrepancies or ambiguities and to
198 ensure a standardized protocol across all papers. We used the following R packages for data
199 management, cleaning and visualization: readxl³⁰, dplyr³¹, CoordinateCleaner³², knitr³³, rmarkdown³⁴,
200 ggplot2³⁵, and cowplot³⁶, as well as custom R code³⁷.

201 In total, our final database consisted of 714 paired temperature offset data points from 74
202 independent studies spread across five continents. Our full database with all variables used in the
203 analyses, as well as all source code, is reported in ref. 37.

204

205 Predictor variables

206 Apart from the temperature variables, we also extracted the following attributes for each offset value
207 and/or study, if available in the original source article:

- 208 • *Location*: Latitude, longitude and elevation (meters above sea level).
- 209 • *Biome*: Based on the geographical coordinates, we classified each site into one of the
210 following three biomes: tropical (latitude was between 23.5°S and 23.5°N); temperate
211 (latitude was between 23.5° and 55°); or boreal (latitude was higher than 55°).

- 212
- *Vegetation type*: Based on the original source article, or, if needed, additional sources (e.g. 213 other papers from the same study site and/or authors), the forest type was classified into 214 each of three categories: deciduous (if dominant tree species was deciduous; 1 in dataset via 215 ref. 37); evergreen (if dominant tree species was evergreen; 2); or mixed (3).
 - *Study length*: number of days during which temperatures were measured, ranging from 1 day 216 to 10 years. 217
 - *Forest density*: We extracted for each study site, if available, any of the following variables 218 relating to forest density: canopy cover (%); tree basal area ($\text{m}^2 \text{ha}^{-1}$); tree density (number ha^{-1}); 219 and leaf area index (LAI). Each of the above-described variables was available for a 220 minority of offset values: 16 % for canopy cover, 23 % for basal area, 7 % for tree density 221 and 8 % for LAI. For reasons of paucity of these data, we do not consider these variables 222 further in our analyses, but the raw data are available in ref. 37. 223
 - *Forest height*: We extracted for each study site, if available (39 % of offset values), the height 224 of the dominant tree individuals (in meters). 225
 - *Topographic heterogeneity and distance to the coast*: because of known effects of topography²⁴ on 226 microclimates, we also extracted topographic heterogeneity using raster layers derived from 227 the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) at 250 m 228 resolution³⁸. We here focused on two variables that capture topographic heterogeneity within 229 a 1 km^2 pixel around each pair of measurements (forest and macroclimate outside forest): (i) 230 the standard deviation of elevation values aggregated per 1 km^2 (further referred to as 231 ‘elevational variation’), and (ii) the median of the topographic position index (TPI) values at 232 1 km resolution. The TPI is the difference between the elevation of a focal cell and the mean 233 of its eight surrounding cells. Positive and negative values correspond to ridges and valleys, 234 respectively, while zero values correspond to flat areas³⁸. Finally, we also extracted the 235

236 distance from each pair of measurements (forest and macroclimate outside forest) to the
237 nearest coastline.

- 238 • *Season of sampling*: Temperature measurements were classified as having taken place during
239 the growing season, the non-growing season, or whether the whole year was sampled
240 (annual). This was aggregated based on reported meteorological seasons and/or climate
241 information in the original study. The dry and winter season were classified as the non-
242 growing season in tropical and temperate biomes, respectively.
- 243 • *Height of the sensor* (continuous variable, in meters above or below the soil surface): positive
244 for aboveground, negative for belowground sensors. While soil temperatures obviously do
245 not reflect macroclimate temperatures, they still allow for a comparison of forests' thermal
246 buffering capacity on soil organisms and processes. The effects of macroclimate
247 temperatures on the offset were similar when only considering sensors placed > 0 cm above
248 the soil surface.
- 249 • *Macroclimate temperature anomalies*: We calculated the difference between each macroclimate
250 temperature and the long-term average temperature for a given site. This was done in order
251 to test if the increase in temperature offset with warmer macroclimate temperatures was due
252 in part to temporal variation in macroclimate, rather than only spatial variation.
253 Macroclimate temperatures are thus compared to a common baseline. Using these
254 temperature anomalies, we asked how the magnitude of the thermal offset capacity of forests
255 varies along a gradient of deviations from long-term temperature averages, analogous to
256 IPCC definitions of climate change⁴. We used 1970-2000 as reference period to compare our
257 macroclimate temperatures outside forests against a common base period. Location-specific
258 long-term averages (1970-2000) of mean annual temperatures were extracted from

259 WorldClim version 2 at 30 arc-second spatial resolution (approximately equivalent to 0.86
260 km² at the equator) for each study site³⁹.

261

262 Data analyses

263 To report summary statistics of the thermal offset capacity of forests globally (Supplementary Table
264 1), two contrasting approaches were adopted. First, the raw mean, median and quantiles were
265 calculated. Then, we carried out a multilevel modeling framework using intercept-only linear mixed-
266 effects models (LMMs) without fixed predictor variables but with ‘*study*’ as a random intercept term
267 to account for pseudo-replication in some of the 74 selected studies. The intercept of intercept-only
268 models represents the average magnitude of the thermal offset of forests while accounting for the
269 non-independence among replicates from the same study. When fitting our intercept-only LMMs,
270 we used the restricted maximum likelihood method in the *lmer* function from the *lme4*-package⁴⁰ as
271 recommended by Zuur et al.⁴¹.

272 Applying a conventional meta-analytical model *sensu stricto* with weighting of different
273 observations by means of variance estimates⁴² was not possible here: an estimate of uncertainty
274 (standard error, deviation, coefficient of variation or confidence intervals) of the offset values was
275 reported for only a small minority (13.6 %) of offset values included in our database.

276 Next, we assessed how macroclimate temperatures and macroclimate temperature anomalies
277 predicted variation in the temperature offset of forests globally. As above, we fitted LMMs with
278 macroclimate temperatures and macroclimate temperature anomalies as fixed effects and ‘*study*’ as a
279 random effect using restricted maximum likelihood in the *lmer* function from the *lme4*-package⁴⁰. We
280 also performed χ^2 -tests by comparing the univariate LMM including a single predictor with the

281 baseline intercept-only model⁴¹. Goodness-of-fit was determined by calculating marginal and
282 conditional R² values following ref. 43 using the *r.squaredGLMM* function in the *MuMIn*-package⁴⁴.

283 We also determined how variables such as absolute latitude, biome, elevation, vegetation type,
284 distance to the coast, the elevational variation and topographic position, season, and sensor height
285 influenced variation in the offset of forests, and how they interacted with macroclimate
286 temperatures. We first ran seven separate univariate LMMs, one per predictor variable as a fixed
287 effect in our LMMs. As earlier, we again fitted LMMs with a random effect term ‘*study*’ using
288 restricted maximum likelihood in the *lmer* function from the *lme4*-package⁴⁰. In order to test
289 interactions, we finally also ran LMMs with two predictor variables each: the macroclimate
290 temperature and each of these seven other predictors (i.e. one-by-one of these seven variables *
291 macroclimate temperature); for the sake of simplicity, higher level interactions were not considered
292 (Supplementary Table 6).

293 Finally, the linearity of the relationship between the temperature offset and macroclimate
294 temperatures was tested with General Additive Mixed Models with the *gamm*-function in the *mgcv*-
295 package⁴⁵ and again *study* was added as random term (Supplementary Fig. 4). Our main findings were
296 robust to the decisions to (i) analyze understory temperatures as the response variable against
297 macroclimate temperature as a fixed effect in LMMs, instead of intercept-only LMMs based on
298 offset values (Supplementary Fig. 3), and (ii) add random intercepts into LMMs, instead of random
299 slopes (Supplementary Table 7). Omitting a few outlier values from a single study¹²⁰ from the
300 analyses also did not affect our conclusions (Supplementary Table 8).

301 All analyses were performed in R version 3.4.4 (ref. 46) and all retained papers are in the
302 reference list⁴⁷⁻¹²⁰. All raw data and code are available in ref. 37. Full results of the statistical analyses
303 are reported in Supplementary Tables 1-8. We followed best practices for reporting meta-analyses

304 recommended by the PRISMA guidelines¹²¹ and included a flow diagram summarising the search
305 criteria in Supplementary Fig. 8.

306 **Acknowledgements**

307 PDF received funding from the European Research Council (ERC) under the European Union's
308 Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833), KV
309 through ERC Consolidator Grant PASTFORWARD 614839, FRS by a postdoctoral fellowship
310 from the Spanish Ministry of Economy and Competitiveness (FPD-2013-16756), FZ by the Swiss
311 National Science Foundation (project 172198) and MV by the Natural Sciences and Engineering
312 Research Council, Canada.

313 **Author contributions**

314 PDF, FZ and JL conceived and designed research. PDF, FZ, JL and FRS assembled and revised the
315 database, and analyzed the data. All authors compiled data and wrote the manuscript.

316 **Competing interests**

317 The authors declare no competing interests.

318 **Materials and Correspondence**

319 Correspondence and requests for materials should be addressed to P.D.F.

320 **Data availability**

321 The datasets and code generated and analysed during the current study are available in the figshare
322 repository³⁷, with the identifier 10.6084/m9.figshare.7604849

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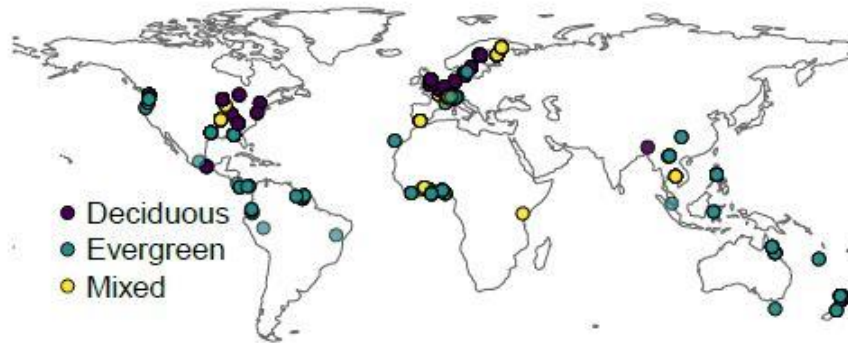
589 **Figure Legends**

590 **Fig. 1 | Forests buffer temperatures under canopies globally.** **a**, Distribution of the 98 study
591 sites and their vegetation type (deciduous, evergreen or mixed forests). **b**, Histograms display the
592 714 paired temperature offset values for maximum (T_{\max}), mean (T_{mean}) and minimum (T_{\min})
593 temperatures. Maximum and mean temperatures are consistently cooler, and minimum temperatures
594 consistently warmer, within forests compared to macroclimate temperatures. Offsets were always
595 calculated as temperatures inside minus macroclimate temperatures outside the forest such that
596 negative (positive) values reflect cooler (warmer) forest temperatures. Offset means and standard
597 errors are based on mixed-effects models with study as a random-effect term. Full statistical
598 analyses, data and code are reported in Supplementary Information and ref. 37.

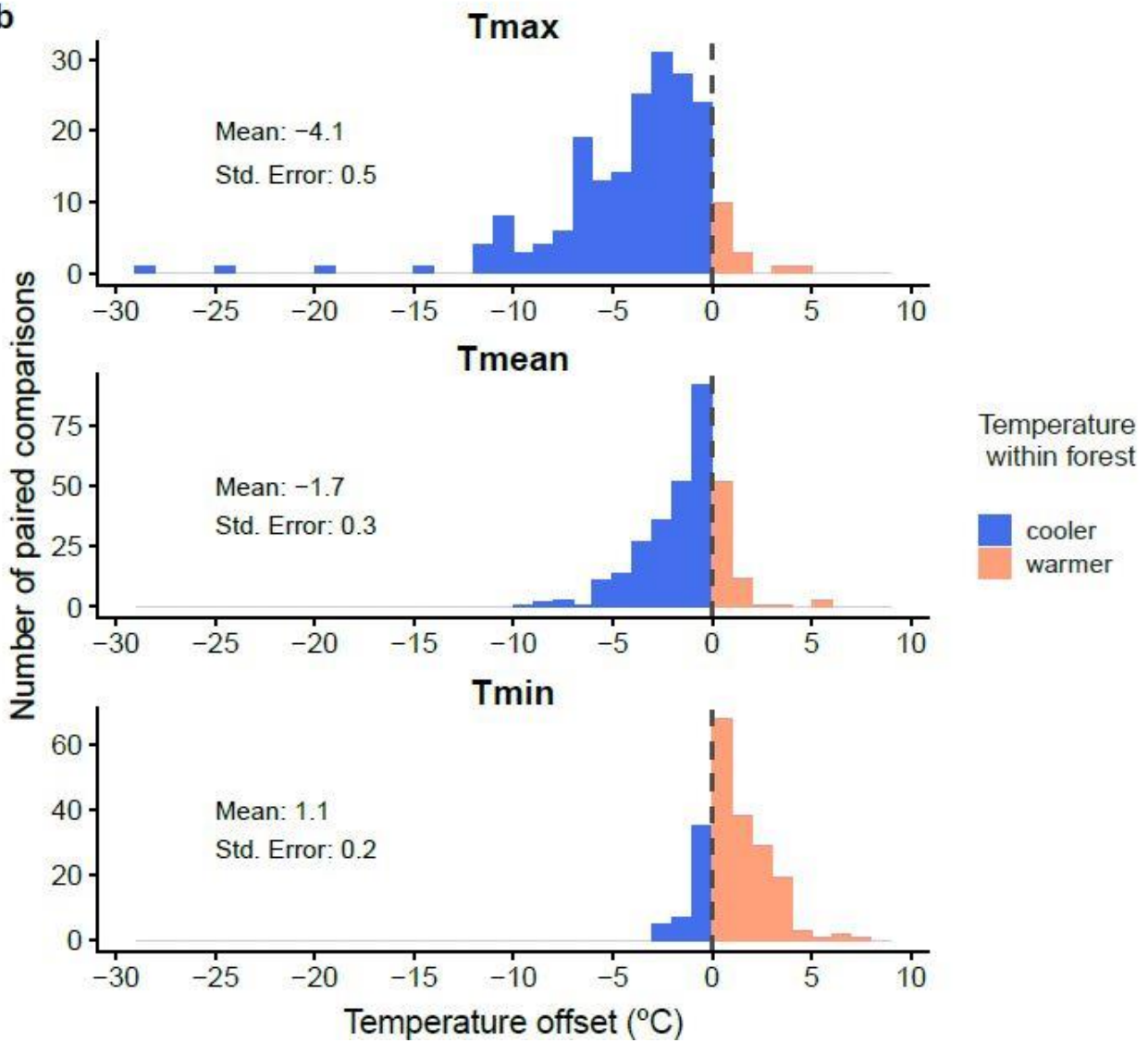
599 **Fig. 2 | Forest temperature offsets under canopies are negatively related to warming air**
600 **temperatures and dependent on the biome.** **a**, The magnitude of the temperature offset within
601 forests depends on ambient macroclimate temperature: the higher the warming, the more offsetting
602 of temperatures (T_{\max} and T_{mean}). For minimum temperatures, positive offsets increase with colder
603 temperatures. **b**, Study sites were classified into boreal, temperate or tropical, based on their latitude.
604 Offset values were always calculated as temperatures inside minus macroclimate temperatures
605 outside the forest such that negative (positive) values reflect cooler (warmer) forest temperatures.
606 Regression slopes, 95% confidence intervals (grey shading), and offset means (red lines), are based
607 on mixed-effects models with study as a random-effect term. Full statistical analyses, data and code
608 are reported in Supplementary Information and ref. 37.

609 Fig. 1 | Forests buffer temperatures under canopies globally

a

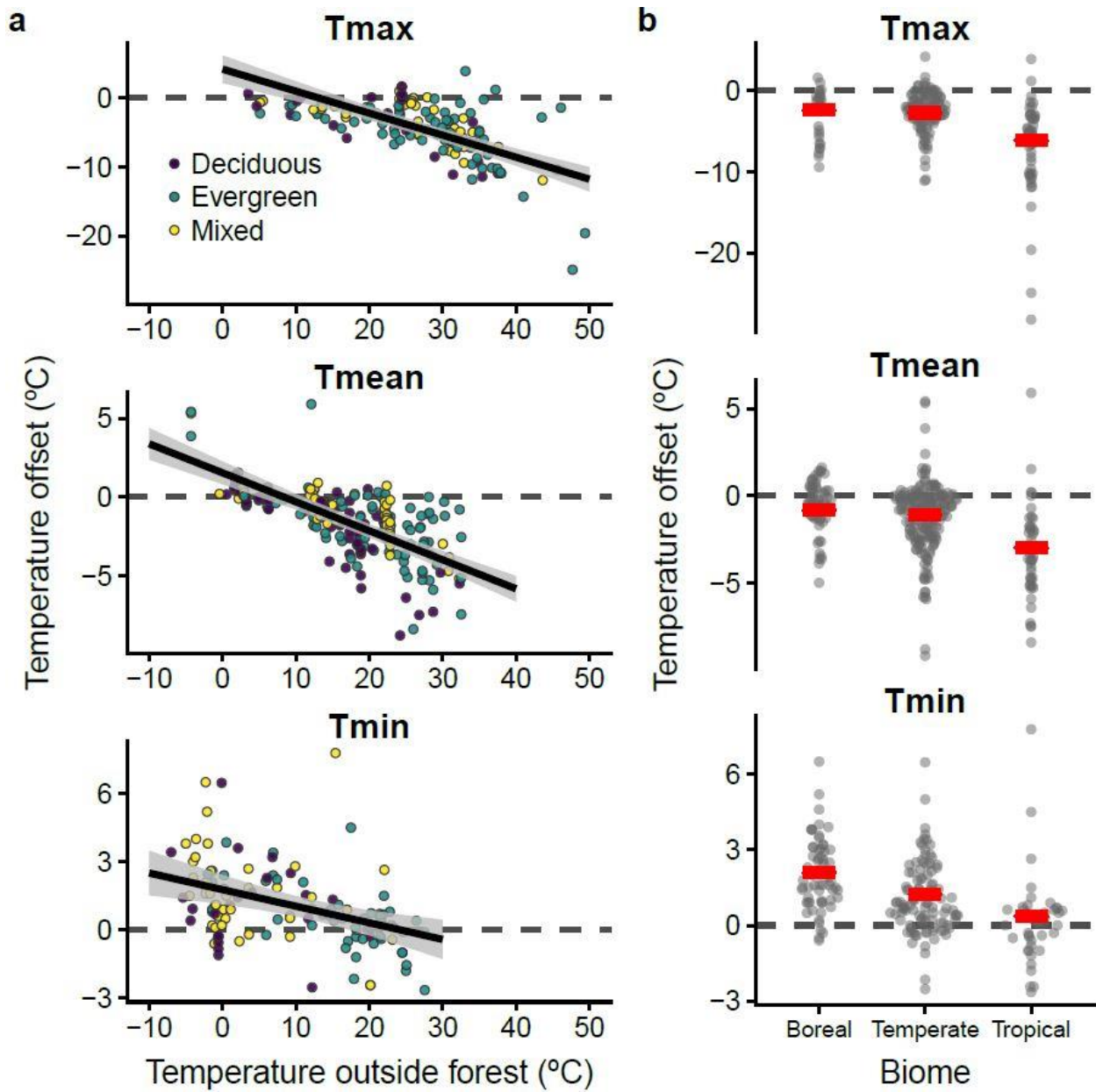


b



610
611

Fig. 2 | Forest temperature offsets under canopies are negatively related to warming air temperatures and dependent on the biome



612